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Reproductive Soldiers in the Termopsidae (Isoptera)

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Abstract.—In addition to nonreproductive soldiers, reproductive soldiers are reported to occur in six of the 17 species of primitive, rotten-wood termites in the world. All three species in the genus *Zootermopsis* from the western United States occasionally produce reproductive soldiers in colonies that are orphaned from the primary reproductives. New records of reproductive soldiers of both sexes are reported from *Zootermopsis laticeps* (Banks). It is suggested that if reproduction by termite soldiers is primitive, then soldiers may have originally evolved by individual-level selection under intracolonial competition among replacement reproductives, rather than by group selection for colony defense.

Polymorphism has evolved in at least 20 different orders of insects (Richards, 1961). Most polymorphism involves color or wing development. But, examples in which one of the morphs is soldier-like are more common than is generally recognized. These include virtually all termites (soldiers lost in Apicotermitinae) in which soldiers are monophyletic (Hare, 1937), about 17% of ant genera in which the soldiers are polyphyletic (Wilson, 1979), some thrips, assassin bugs, bark beetles, fig wasps, and others (Hamilton, 1979), one bee (Houston, 1970), some aphids (Aoki, 1982, 1983), and lammellicorn beetles (Otte and Stayman, 1979). In many of these cases behavioral studies have shown that the primary function of the hypertrophied mandibles of the soldier-like morph is not colony defense but intracolony combat (Hamilton, 1979). Thus it appears that these morphs have evolved by selection pressures resulting from reproductive competition, i.e., social selection, or more specifically intrasexual selection (West-Eberhard, 1981). In view of this it seems significant that the most socially primitive termites have occasional reproductive soldiers. In this paper records of reproductive soldiers in the family Termopsidae are assembled for the first time along with new records in *Zootermopsis laticeps* from Arizona.

REVIEW OF REPRODUCTIVE SOLDIERS IN TERMOPSIDAE

Records of reproductive soldiers are widely scattered through the literature, interspersed among mostly old descriptions of natural history. Consequently these records have never before been assembled. The earliest observations were on *Zootermopsis angusticollis* and *Z. nevadensis* by Heath (1903). He observed three such "monstrosities" and noted that they occurred only when the primary reproductives were absent. All three laid eggs in captivity and these hatched into normal nymphs and workers. Heath later (1907) stated that reproductive soldiers "appeared in small fragments of wood, which have broken off from the main trunk inhabited by an extensive colony . . . ." He regarded them as developmental abnormalities possibly induced by an abnormal "mode of feeding" associated with the disturbed conditions.

Imms (1919) made numerous references to reproductively functional soldiers in his monograph on *Archotermopsis wroughtoni.* He observed that the testes and ovaries of soldiers were normally developed to the same extent as those of the alates before flight and showed no signs of "degeneration or arrestation of development." He found five females with ovaries more developed than those of preflight alates. He stated that "it is likely that all the individuals of that caste [soldiers] are potentially capable of reproduction." He also referred to studies by Müller (1873) on *Calotermes* [=*Kalotermes*] *canellae* and observations on *C. nodulosus* and *C. rugosus* that soldier ovaries are developed almost to the same extent as in the winged caste but have the spermathecae undeveloped. Thus he felt that a general trend existed from primitive termite soldiers with well developed and sometimes functional gonads, through more advanced soldiers with gonads reduced "primarily by an arrestation of development," to the most advanced soldiers with a "variable amount of atrophy or degeneration."

Heath (1927) added an additional observation of a "fertile soldier," bringing to four the number of specimens he had observed. He also made actual observations of copulation between the female fertile soldier and a male neotenic reproductive and again observed ovipositing of eggs and hatching of normal progeny. Heath (1928) reported observation of 14 additional fertile soldiers of *Z. nevadensis* all of which had been collected from fragments of a broken limb of *Pinus radiata.* He illustrated the fertile soldiers' relatively small heads compared to normal soldiers and described their tendency to congregate with neotenics rather than to "move about from place to place" in the manner of typical soldiers.

Castle (1934) also observed fertile soldiers of both sexes of *Z. nevadensis* from colonies collected in the field and in isolated groups in the laboratory. He stated that they developed in groups having neither soldiers nor functional reproductives. Light (1943) stated that in *Zootermopsis angusticollis* "Intercastes such as wing-padded soldiers, and various soldier-nymphal-neotenic or alate-soldier-nymphal-neotenic intergrades indicate that several of these influences may affect the terminal characteristics of a single individual." Light (1944) reported experiments in which typical soldiers when isolated were found incapable of transformation to reproductive soldiers, an indication that reproductive soldiers do not develop through the transformation of typical soldiers.

Zootermopsis and *Archotermopsis* belong to the termopsid subfamily Termopsinae, in many respects the most primitive of living termites (Emerson, 1933, 1955). Reproductive soldiers have also been reported from the monogeneric subfamily Stolotermitinae. Morgan (1959) referred to small-headed "emergency soldiers" which develop under disturbed conditions in *Stolotermes ruficeps.* It seems likely that these are reproductive soldiers. Gay and Calaby (1970) reported that "soldiers with obvious wing pads, and functional gonads have been demonstrated in male soldiers . . ." of *Stolotermes brunneicornis.* This has been confirmed by J. A. L. Watson (pers. comm.) who observed "soldiers that on histological grounds appear to be fertile in *Stolotermes brunneicornis* (Hagen) from Tasmania . . . ." Emerson and Krishna (1975) state that "In the most primitive termites [presumably termopsids] soldiers occasionally lay unfertilized eggs which may hatch into parthenogenetic nymphs."

New Records of Reproductive Soldiers in *Z. laticeps*

Recently I have made observations of reproductive soldiers in *Zootermopsis laticeps* from Arizona. The first individual was found in a 1.5 meter section of willow about 30 cm in diameter which had been sawn from a standing tree near Tumacacori, Arizona, in July, 1982 and stored at ambient conditions in Tucson until extracted on November 29, 1982. The log fragment, which contained only a portion of the original colony and was orphaned from the primary reproductives, had the following population at the time of extraction: 779 immatures of various instars, 8 normal soldiers, 3 neotenic females, and 1 small-headed male reproductive soldier (see Fig. 1). Because the small-headed soldier resembled Heath's (1928) illustration of a fertile soldier in *Z. nevadensis,* it was dissected to ascertain the condition of its reproductive system. The reproductive tract proved to be well developed and apparently functional on the basis of size. In contrast, the reproductive tracts of the normal soldiers from the same colony were completely undeveloped. In comparison to the reproductive tract of a mature primary king, from another colony with a population of 913 individuals, the width and length of the vasa deferentia and the width, length, and number of accessory gland tubules were comparable. The testicular diameter of the reproductive soldier was even greater than that of the primary king (Fig. 2). Unfortunately, no attempt was made to find sperm.

Another colony of *Z. laticeps* was collected from a willow branch near Rio Rico, Arizona, on March 4, 1984. From this colony four groups were set up in petri dishes: (Group #1: 11 nymphs with wing pad abscission scars; Group #2: 57 short-wing-padded (N1 and N2) nymphs; Group #3: 52 long-wing-padded (N3) nymphs; Group #4: 66 workers and 5 soldiers). A total of 3, 12, 2, and 8 neotenics developed within these groups, respectively. Over an observation period of 160+ days, first eggs appeared from 72–91 days and first larvae after 131 days. Presoldiers appeared only in Group #2. Four presoldiers developed between day 16 and 20 and transformed to soldiers between day 34 and 46. All four were dissected on day 103. The smaller two were females, whose ovary development was comparable to neotenics of the same age. The other two soldiers were a male and a female and had underdeveloped gonads. As with the field-collected specimen the two reproductive soldiers had noticeably smaller heads than typical soldiers.

Summary

The Termopsidae contains 17 species in 5 genera and 3 subfamilies. Six species in 3 genera and in 2 subfamilies have been reported to have reproductive soldiers or at least soldiers with apparently functional gonads. Table 1 gives a full listing of the family Termopsidae with all references to reproductive soldiers. Three species whose biologies have been moderately investigated and yet are unknown to possess reproductive soldiers are *Porotermes adamsoni* (Mensa-Bonsu, 1976; Lenz, 1985), *P. planiceps* (Coaton and Sheasby, 1976), and *Stolotermes africanus* (Coaton and Sheasby, 1978). The remaining species without reports of reproductive soldiers have not been well studied. Reproductive soldiers may be expected in additional termopsid species when their biologies are more closely examined.

The possible relevance of reproductive soldiers to theories on the origin to

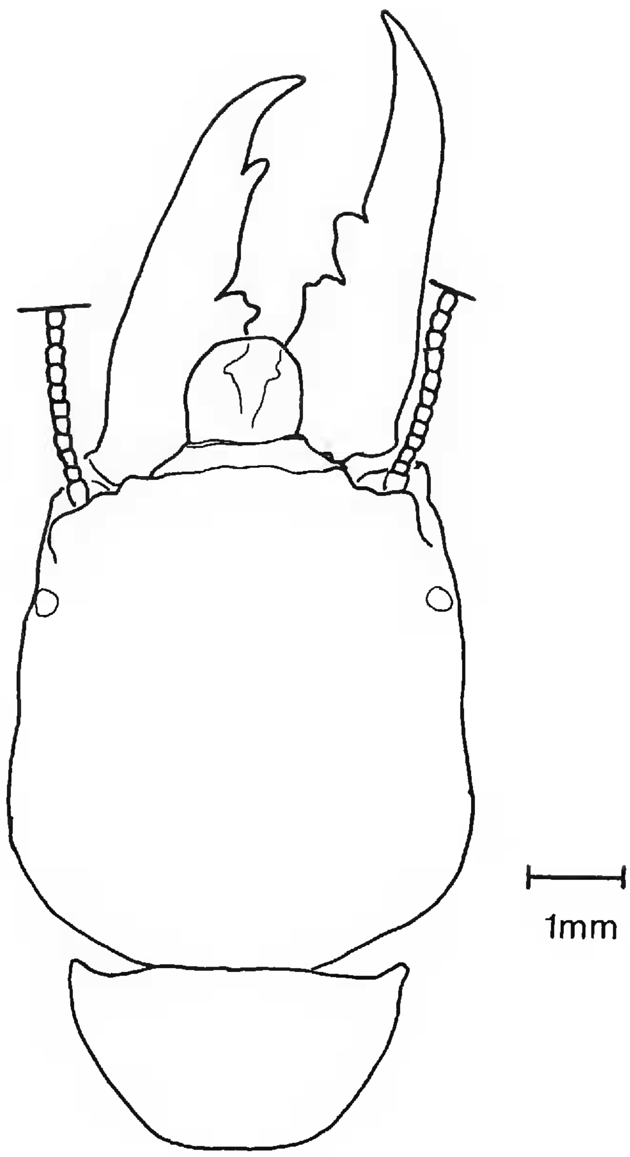

Fig. 1A

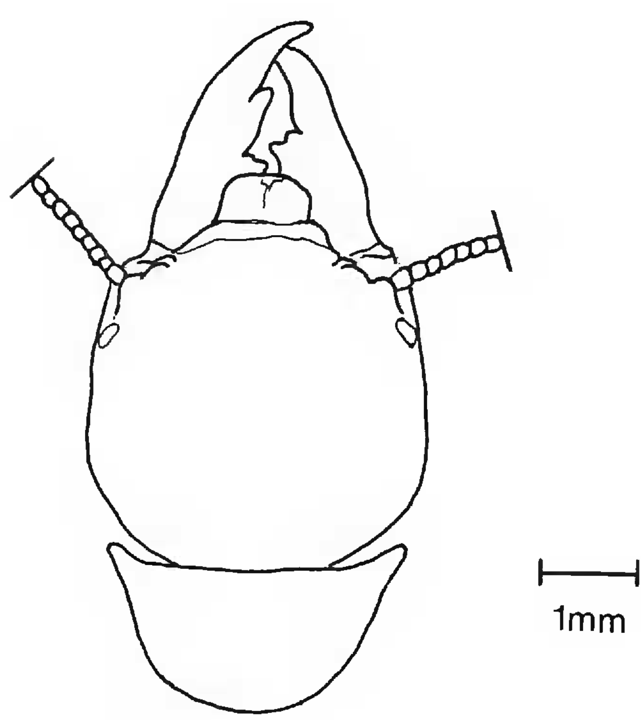

Fig. 1B

Figure 1. A. Head and pronotum of a typical non-reproductive soldier of *Zootermopsis laticeps* from Colony #3 (right mandible slightly disjointed). B. Head and pronotum of male reproductive soldier of *Zootermopsis laticeps* from Colony #3 collected near Tumacacori, Arizona (see text).

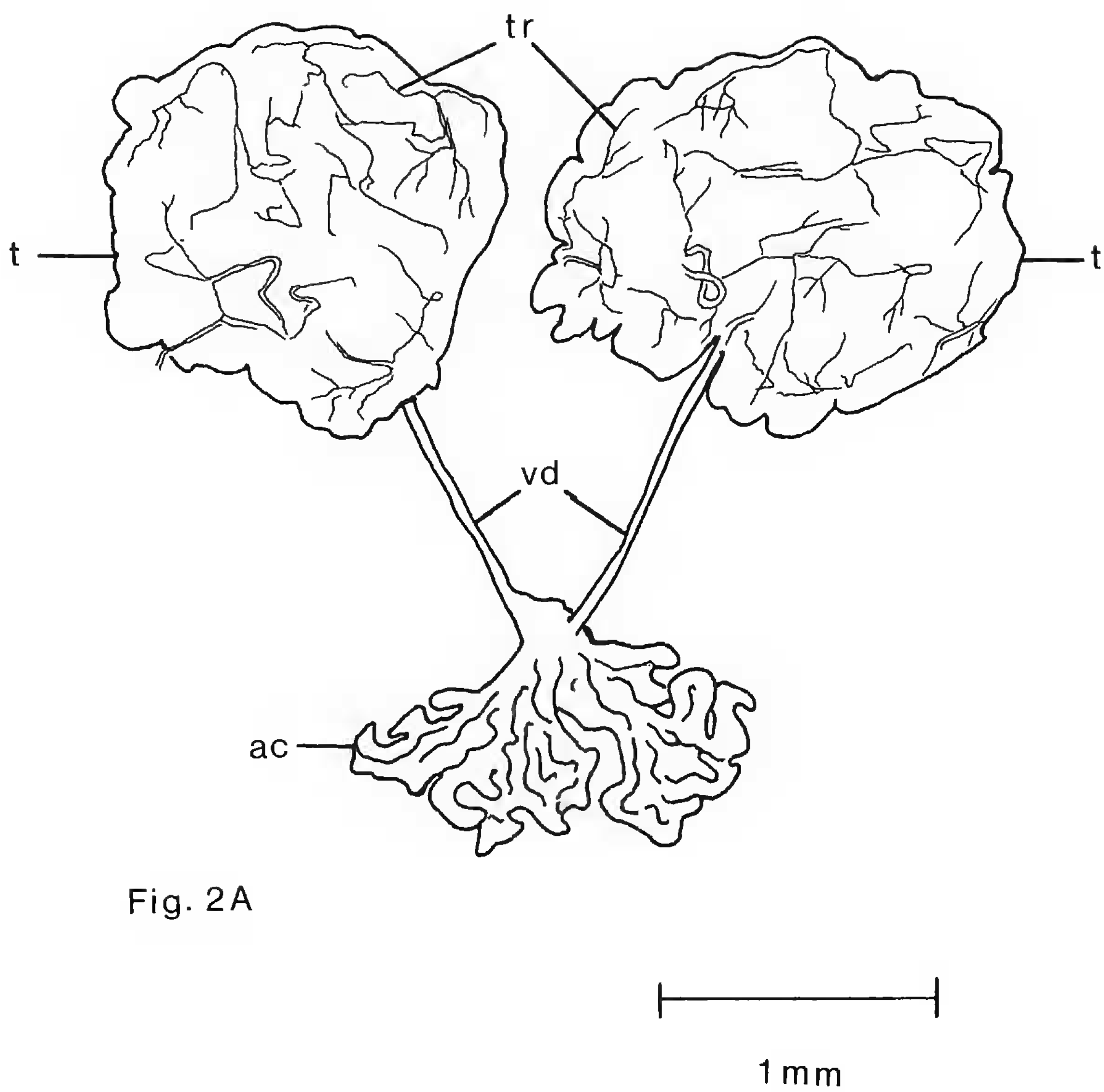

Fig. 2A

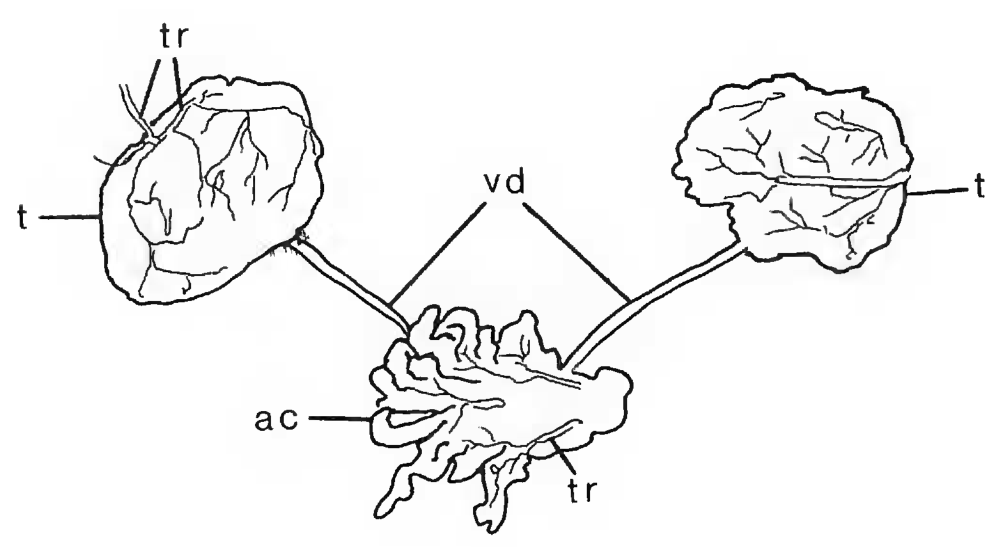

Fig. 2B

Figure 2. A. Testes (t), vasa deferentia (vd), and accessory glands (ac) of reproductive soldier of *Zootermopsis laticeps* from Colony #3 (see Fig. 1B), trachea (tr). B. Testes, vasa deferentia, and accessory glands of king of *Zootermopsis laticeps* from Colony #4 with population in excess of 900 individuals (diagrams A and B to same scale).

Table 1. Synopsis of Termopsidae with notes and references to species having records of probable reproductive soldiers.

Termopsidae

Termopsinae

1. *Archotermopsis wroughtoni* soldiers with functional gonads. Imms (1919)
2. *Archotermopsis deodare* (=*A. wroughtoni*?) no information
3. *Hodotermopsis japonicus* no information
4. *Hodotermopsis sjostedti* no information
5. *Zootermopsis angusticollis* fertile soldiers. Heath (1903, 1907, 1927); Castle (1934); Light (1943, 1944); S. L. W. Greenberg (pers. comm.)
6. *Zootermopsis nevadensis* fertile soldiers. Heath (1903, 1907, 1927, 1928); Castle (1934); Light (1943, 1944); one apparent example (not dissected), M. I. Haverty (pers. comm.)
7. *Zootermopsis laticeps* reproductive soldiers

Stolotermitinae

8. *Stolotermes africanus* no information
9. *Stolotermes australiensis* no information
10. *Stolotermes brunneicornis* soldiers with functional gonads. Gay and Calaby (1970); J. A. L. Watson (pers. comm.)
11. *Stolotermes inopinatus* no information
12. *Stolotermes queenslandicus* no information
13. *Stolotermes ruficeps* emergency soldiers. Morgan (1959)
14. *Stolotermes victoriensis* no information

Porotermitinae

15. *Porotermes adamsoni* reproductive soldiers not reported
16. *Porotermes planiceps* no information
17. *Porotermes quadricollis* no information

termite soldiers must await a better understanding of the conditions under which they develop and behavioral studies to determine whether they engage in combat with other replacement reproductives. There is reason to believe that reproductive soldiers do fight since lethal siblicidal fighting is known to occur between replacement reproductives of several lower termites (see references in Myles and Chang, 1984).

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